

Impact of salinity and nutrients on salt marsh stability

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Abstract. Belowground growth in coastal plants is critical for marsh stability and the ability of coastal wetlands to keep pace with sea-level rise. Quantifying the effects of nutrient loading on belowground plant growth is an ongoing controversy in wetland research, with previous experiments demonstrating both positive and negative impacts. Moreover, salinity may also decrease belowground growth through sulfide toxicity, or plants may increase root growth to oxidize sediments and respond to sulfide stress. Because salinity influences plant nitrogen assimilation and sediment nitrogen retention, salinity and nitrogen may interact to influence belowground plant growth. We sampled an urban-to-rural land-use gradient of 11 *Spartina alterniflora* marshes on Long Island, New York, to look for correlates of belowground biomass. We found that belowground biomass was related positively to salinity and negatively to extractable nitrogen content in sediments. Total belowground plant biomass was reduced by 60–70% in high-nitrogen marshes and enhanced by as much as 70% in high-salinity marshes. Further, we found no evidence of interaction between salinity and nitrogen, indicating that these factors were independently related to belowground plant growth. Our results indicate that chronic eutrophication and increasing salinity resulting from sea-level rise are likely to have opposing effects on future marsh stability.

Key words: belowground biomass; eutrophication; multiple stressors; sea-level rise; shoreline stability; *Spartina alterniflora*.

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INTRODUCTION

The future resilience of many ecosystems depends on their response to a range of stressors that vary simultaneously over space and time (Staudt et al. 2013). Models that account for the concurrent impacts of these stressors will be essential to maintain services provided by these ecosystems. This fact is especially true for coastal salt marshes that will face multiple spatially heterogeneous stressors going forward, including coastal eutrophication and sea-level rise (Crain et al. 2008). Salt marshes provide services such as shoreline stabilization, flood and storm surge protection, and maintenance of coastal water quality (Zedler 2003, Costanza et al. 2008, Gedan et al. 2011). Consequently, understanding how marshes respond to multiple stressors is critical for the health and economic well-being of coastal communities worldwide (Millennium Ecosystem Assessment 2005). To keep pace with sea-level rise, marshes must accumulate sediment and organic matter, while resisting erosion from waves and storm surges. Both features of resilient marshes depend on well-developed root systems (Nyman et al. 2006, Perillo et al. 2009, Pratolongo et al. 2009). Despite a long history of study (Valiela et al. 1976, Mendelssohn and Morris 2000, Wigand et al. 2009, Graham and Mendelssohn 2014), the relationships between abiotic

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factors and root-mass production and accumulation remain poorly understood.

One of the abiotic factors influencing root growth in coastal marsh vegetation is the availability of inorganic nitrogen. Relative to preindustrial levels, human activities have doubled the global inputs of fixed nitrogen, a limiting nutrient in many coastal marshes (Vitousek et al. 1997, Mendelssohn and Morris 2000, Bertness et al. 2002, Millennium Ecosystem Assessment 2005). Marshes receive excess nitrogen as acid precipitation, sewage waste, and fertilizer runoff (Seitzinger et al. 2005). In response to fertilization, plants generally allocate a lower proportion of their growth to belowground biomass because they require fewer roots to acquire the nutrients needed to support growth of photosynthetic tissues aboveground (Ericsson 1995). Reductions in living root mass have been observed in nutrient enrichment studies and were often accompanied by a decrease in sediment stability (Turner et al. 2009, Kearney et al. 2011, Deegan et al. 2012, Watson et al. 2014). However, physiological models of marsh vegetation and other enrichment studies have suggested that nitrogen additions can result in greater growth of belowground biomass and can also lead to increased sediment capture due to enhanced aboveground biomass and stem density (Howes et al. 1986, Morris et al. 2002, Darby and Turner 2008, Anisfeld and Hill 2012, Fox et al. 2012, Graham and Mendelssohn 2014). An increase in belowground biomass with nitrogen fertilization is expected if the increase in total growth compensates for lower relative allocation of growth to roots and rhizomes (Morris et al. 2013). Alternatively, nitrogen fertilization could result in limitation by another nutrient, such as phosphorus, which would require that extensive root systems be maintained (Turner 2011).

In the future, responses to nitrogen will occur against a backdrop of changing porewater salinity. Salinity may increase with increasing sea levels as seawater intrudes into brackish marshes. Alternatively, it may decrease as greater precipitation increases freshwater discharge from groundwater and rivers (Craft et al. 2008). The impacts of such changes on wetlands are potentially complex. Increasing salinity correlates with a higher concentration of sulfate ions, which can be reduced to hydrogen sulfide in low redox marsh sediments (Mendelssohn and Morris 2000). Because sulfide is toxic to plants, root production is generally expected to decline as salinity increases in anoxic marsh sediments (Linthurst and Seneca 1981, Mendelssohn and Morris 2000). However, marsh plants may also increase root density in the presence of sulfide to introduce more oxygen into sediments, thereby facilitating oxidation of sulfide to non-toxic sulfate (Armstrong et al. 1994). Salinity and nitrogen may also interact to affect marsh plants (Mendelssohn and Morris 2000). Salinity is known to directly inhibit ammonium assimilation by plants (Bradley and Morris 1990) while increasing ammonium fluxes to porewater from sediments (Giblin et al. 2010). Field evidence for effects of salinity on belowground growth is sparse and does not clearly support a positive or negative relationship between the variables, nor is it sufficient to address potential interactions with nutrient availability (Drake and Gallagher 1984, Howes et al. 2010).

We examined the simultaneous influences of salinity and sediment nutrient availability on belowground growth of Spartina alterniflora across 11 coastal salt marshes that span an urban-torural land-use gradient from western to eastern Long Island, New York (Fig. 1). The study sites represent a 50- to 100-yr chronosequence of development from forested to agricultural-to-urban land-use types, a series of land-use transitions that reflects development patterns occurring worldwide (Millennium Ecosystem Assessment 2005). Using 430 observations of total belowground biomass collected in June and August over two years, we constructed linear models to assess the ability of salinity and inorganic nutrients to explain sitelevel variation in belowground biomass. Because aboveground plant growth has the potential to offset marsh loss by enhancing sediment capture, we also examined the influence of salinity and nutrients on aboveground plant biomass. The primary goal of our study was to identify the major correlates of marsh stability, in the hopes of identifying those factors that have most affected marsh development over multidecadal scales.

MATERIALS AND METHODS

Long Island, New York, represents a wellestablished gradient ranging from high-intensity land use in urban areas of western Long Island near New York City to comparatively

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Fig. 1. (A) Research locations on Long Island, New York, ranging from high human population density in

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(Fig. 1. Continued)

western Long Island to rural areas in eastern Long Island (United States Geological Survey [USGS] 2010). Marshes varied in (B) extractable inorganic nitrogen and (C) salinity. Error bars show standard error for site-level means (n = 10); the moving averages (solid lines) and confidence regions (shaded areas) were computed using a loess smoothing function.

low-intensity land use in agricultural and forested areas of eastern Long Island (O'Shea and Brosnan 2000, Scorca and Monti 2001, Monti and Scorca 2003, Benotti et al. 2007). Whereas pre-development nitrogen fluxes to Long Island marshes originated almost entirely from groundwater, post-development fluxes are dominated by overflows from sewage treatment and drainage from septic systems and cesspools (Ayers et al. 2000, Benotti et al. 2007, Gobler 2016). Fertilization of golf courses, parks, agricultural areas, and lawns also contributes a small amount to total nitrogen loads, including legacy effects from historically extensive duck farms in eastern Long Island (Ayers et al. 2000, Benotti et al. 2007, Gobler 2016). Because wastewater is the largest source of nitrogen (at least 70%), total nitrogen inputs are generally found to be greatest in areas of highest human population density (United States Geological Survey [USGS] 2010). Additionally, variation in tidal range and stream discharge among the various Long Island embayments offered a high probability that average salinity would vary among sites independently of variation in nitrogen (Scorca and Monti 2001, Monti and Scorca 2003).

Eleven salt marshes on Long Island, each dominated by a near monoculture of Spartina alterniflora, were selected for sampling (Fig. 1) to examine the effects of nutrient availability and salinity on aboveground and belowground plant biomass. Sampling was conducted in June and August of 2012 and 2013, times chosen to correspond to the period of active plant growth and the period just after peak biomass was attained. This allowed us to address potential seasonal differences in correlations between abiotic variables and standing plant biomass resulting from new plant growth. For each marsh site, ten 25×25 cm quadrats were randomly placed at least 1 m apart, five within the marsh platform where short-form S. alterniflora are typically found, and five near a creek edge where tall-form S. alterniflora are more common. Within each quadrat, we clipped all aboveground

vegetation. Clippings were dried at 50°C for at least 48 h and weighed to determine aboveground biomass. A sediment core (diameter ≈ 5 cm, length ≈ 10 cm) was taken from the center of each quadrat to determine total belowground plant biomass. Total belowground biomass was determined by wet sieving core samples through a 1000-µm sieve and removing non-vegetative material by hand. Because the living and dead fractions of belowground plant material were impossible to distinguish for all of our samples, our belowground biomass measurements necessarily include the total contribution of living and dead roots and rhizomes to total belowground plant material in marsh sediments. Hereafter, this variable is referred to as "belowground biomass" for simplicity.

We collected sediment porewater from each quadrat using vacuum sippers (Kolker 2005). Samples were transported on ice and frozen at -20°C until analysis of salinity with a refractometer and analysis of ammonium and nitrate content using standard methods (Jones 1984, Parsons et al. 1984). Nitrate and ammonium were summed and reported as dissolved inorganic nitrogen (DIN). In 2013, an additional 5-g sediment sample from each plot was extracted with 10-mL 2N KCl and analyzed for ammonium, nitrate, and phosphate contents (Jones 1984, Parsons et al. 1984, Wetzel and Likens 2000).

Models were constructed to predict patterns in aboveground and belowground biomass using JMP 7.0 statistical software (JMP(R) 1989–2007). Initial models were constructed as an ANCOVA, with sampling time included as a categorical predictor and nutrients and salinity as continuous predictors. All potential second-order interactions among predictor variables were also included. A step-wise linear regression was performed to select final models, with a threshold of P = 0.10for variables to enter or leave models. Interaction terms were eliminated if main effects were not significant. Because all predictor variables were not measured in all years, two separate sets of models were constructed, one containing all predictor variables collected in 2012-2013 (salinity, porewater DIN) and one containing all variables collected in 2013 (salinity, extractable DIN, extractable phosphate). Extractable phosphate and all porewater nutrient measurements were log₁₀-transformed to satisfy assumptions of normality. Measurements in tall- and short-form S. alterniflora were not found to differ systematically in total aboveground or belowground biomass and were pooled such that analyses were conducted on mean values for sites and sampling times. Relationships between predictor variables and biomass were calculated and plotted in R version 3.0.3 (R Core Team 2012) as standard major axis (SMA) regressions to account for appreciable measurement error in both dependent and independent variables. Details of analyses and R code are provided in Appendix S1. All data and metadata are available in Data S1 and MetaData S1, respectively. Tests with P-values <0.05 were considered statistically significant, while values between 0.1 and 0.05 were considered marginally significant.

Results

Among variables measured in June and August 2013, total belowground biomass was negatively related to extractable DIN (P = 0.013; Table 1, Fig. 2A) and positively related to porewater salinity (P = 0.056; Table 1, Fig. 2B). Mean belowground biomass differed between sampling times (P = 0.015; Table 1). However, the slopes relating belowground biomass to salinity or DIN did not

differ between sampling times (Fig. 2A, B), as the interactions between these variables and sampling time were not significant (P = 0.71 and 0.45, respectively). Aboveground biomass was positively related to sampling time only (Table 1); however, we did observe a trend in which aboveground biomass increased with DIN availability (Fig. 2C). Overall, for the 2013 data, we detected a 60-70% reduction in belowground biomass and a 70% increase in aboveground biomass with increasing DIN availability at the site level (Fig. 2A, C). Additionally, belowground biomass was found to increase with increasing salinity by as much as 70%. No interactions between salinity and DIN were retained in final models, indicating that the effects of salinity and DIN were additive (Table 1). Overall, we were able to explain over 53% of the total variation in belowground biomass with extractable DIN, salinity, and season. Not surprisingly, the difference between the periods of biomass accrual (June) and peak biomass (August) explained 32% of the total variation in aboveground biomass among marsh sites (Table 1).

For the full set of aboveground and belowground biomass measurements (2012–2013), only sampling time, porewater DIN, and salinity were available as independent variables. Salinity was positively related to belowground biomass, and although mean belowground biomass again differed significantly among sampling times, the slope of the relationship was similar among all sampling times (Table 1, Fig. 2B). Differences among sampling times alone explained 56% of the variation in aboveground biomass (Table 1).

Table 1. Best model for predicting belowground and aboveground biomass (g/m²) of *Spartina alterniflora* at the site level.

	Belowground biomass					Aboveground biomass				
Parameter	Model R ²	df	SS	F	Р	Model R ²	df	SS	F	Р
2013 data only	0.53					0.32				
Time		1	2.40×10^6	7.29	0.015		1	3.22×10^{5}	9.59	0.006
Salinity (ppt)		1	1.37×10^{6}	4.16	0.056					
DIN (µmol/L)		1	2.50×10^{6}	7.59	0.013					
Residuals		18	5.94×10^{6}				20	6.72×10^{5}		
2012 and 2013 data	0.31					0.56				
Time		3	5.28×10^{6}	3.96	0.015		3	9.00×10^{5}	16.84	< 0.0001
Salinity (ppt)		1	4.59×10^{6}	10.33	0.003					
Residuals		38	1.69×10^{7}				39	1.59×10^{6}		

Notes: Two sets of models were run, one set initially including all variables measured in 2013, and one including all variables measured in 2012 and 2013. In all cases, interaction terms were non-significant and were removed from final models. df, degrees of freedom; DIN, extractable dissolved inorganic nitrogen; SS, sum of squares.



Fig. 2. (A) Among sites, total belowground plant biomass of *Spartina alterniflora*, including living and dead roots and rhizomes, was negatively associated with extractable inorganic nitrogen content of sediments in June 2013 (slopeSMA = -9.02) and August 2013 (slopeSMA = -8.94). (B) Belowground biomass was positively associated with the salinity of sediment porewater in June 2012 (slopeSMA = 145.6), August 2012 (slopeSMA = 109.4), June 2013 (slopeSMA = 90.11), and August 2013 (slopeSMA = 101.4). (C) Total above-ground biomass showed a positive but non-significant trend with extractable inorganic nitrogen in August 2013 (slopeSMA = 2.75) and June 2013 (slopeSMA = 1.74). (D) Aboveground biomass was not related to salinity. SMA, standard major axis.

Sampling time and salinity explained 31% of the variation in belowground mass for the 2012–2013 dataset. In all cases, porewater nitrogen and extractable phosphate measurements were found to be poor predictors of aboveground and below-ground biomass and were discarded from final models. Among all sampling times, above-ground and belowground plant biomass measurements were uncorrelated among sites and sampling dates (n = 43, r = -0.06, P = 0.72).

Discussion

This work supports the hypothesis that eutrophication due to nitrogen loading exerts a negative influence on belowground biomass, and thus marsh stability, in coastal marshes. This result is consistent with a growing body of evidence suggesting that increasing nutrient availability decreases the amount of growth allocated to roots and rhizomes (Valiela et al. 1976, Deegan et al. 2012, Watson et al. 2014). Notably, most previous studies have been based on relatively shortterm enrichment experiments and have witnessed a response in only the living fraction of belowground biomass. This study is one of the few that has detected a response in total belowground biomass, including both living and dead root material (Morris and Bradley 1999, Wigand et al. 2009). A reduction in total belowground biomass, from both the accumulation and decomposition of dead root matter, is a slow-response variable that is less likely to be detected in short- to moderate-term (i.e., 5-15 yr) experiments. By comparison, the variation in total belowground biomass in Long Island marshes represents a long-term response to 50-100 yr of differences in enrichment and thus reflects the effects of chronic eutrophication on belowground biomass and marsh stability. Notably, a negative relationship between total belowground plant biomass and nitrogen inputs was also observed in a previous study of extant marshes in Narragansett Bay, RI, which were subject to chronic nutrient enrichment; however, this relationship was observed only in higher elevation marshes dominated by Spartina patens (Wigand et al. 2009). Together these findings have important implications for the long-term stability of marshes that are believed to be currently stable under nutrient enrichment.

Sediment capture by marsh plants is not likely to be an important determinant of marsh stability on Long Island and marshes along coastal barrier islands generally, which typically receive lower sediment loads than marshes with large riverine inputs (Darby and Turner 2008, Wigand et al. 2009). Hypothetically, nitrogen fertilization could stimulate aboveground plant growth and more effectively trap suspended particles, offsetting losses in organic matter accumulation (Morris et al. 2002). Our lack of correlation between aboveground and belowground production (P = 0.72) suggests that controls on these responses may be decoupled, which may seem counterintuitive as both are at least weakly associated with DIN (Fig. 2). However, biomass responds to variables other than DIN, such as salinity in the case of belowground biomass (Fig. 2B) or tidal range in the case of aboveground biomass (Steever et al. 1976). Also, as DIN increases, the opposing effects of increasing aboveground and decreasing belowground biomass on sediment retention may depend on a range of variables, including rates of sediment delivery via streams and the strength of tidal and storm surges. In marshes with low sediment deposition, such as in Long Island and other northeastern marshes (Kim and Bokuniewicz 1991, Watson et al. 2014), factors controlling belowground growth and organic matter accumulation are likely to be more important determinants of vertical marsh growth than sediment capture by aboveground biomass.

The nutrient-loading context of Long Island marshes may explain why the responses of plant root variables differed from those observed in some other studies. While DIN had an effect on belowground biomass, we found no evidence of phosphate effects. This difference may result from low N:P ratio in sediment porewater, which never exceeded 15 for any of the sites included in our study, making it extremely unlikely these marshes are phosphorus limited (Verhoeven et al. 1996). In marshes with lower phosphorus availability, nitrogen enrichment may cause plants to become phosphorus limited, and they may allocate more growth to roots to scavenge for phosphate (Turner 2011). The background nutrient supply ratios should be taken into context when comparing results of studies relating eutrophication to marsh vegetation.

The consistently positive effect of salinity on belowground biomass in Spartina alterniflora marshes was the most surprising result we observed (Fig. 2B). This result supports the hypothesis that plants allocate more growth to roots and rhizomes as a stress response, aerating sediments to increase sulfide oxidation and alleviate sulfide stress (McKee et al. 1988). Our results are consistent with one other field study, which found that high-salinity marshes produce more roots and have a higher sediment shear strength than nearby low-salinity marshes (Howes et al. 2010). These results suggest that increasing salinity from sea-level rise may enhance stability of brackish coastal marshes for a given amount of sediment delivery and total production.

Though consistent with previous work showing that nutrient loading negatively impacts root mass, our findings suggest a larger role for salinity in determining total root and rhizome mass than is commonly expected. Our results indicate that eutrophication may reduce marsh stability and that increasing salinity in inland marshes as sea level rises may increase stability of those marshes. Because high sulfide concentrations inhibit nitrogen assimilation (Mendelssohn and Morris 2000), we expected an interaction between the effects of salinity and DIN on belowground biomass. However, our analysis determined that salinity and DIN acted independently and that their combined effects are therefore additive. Therefore, though their effects on total belowground biomass are likely to exhibit complex spatial signatures over time, the fact that they act independently and consistently means that we should be able to predict a significant proportion of the variation using relatively simple biological relationships. Given sufficient knowledge of hydrology and sediment load, a holistic management approach that accounts for hydrological and chemical determinants of marsh growth may well be within reach. Such an approach would enhance our ability to assess the stability of marshes under future scenarios of sealevel rise and eutrophication.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2. 2010/full